BEHAVIOR OF SUMMERING GRAY WHALES

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The behavior of gray whales was studied near St. Lawrence Island, Alaska, in July and September 1982. Most behavior involved apparent feeding near the bottom, as evidenced by mud plumes around surfacing whales, and kittiwakes landing near whales at the surface. There was little socializing by whales in July, but more toward the end of September.

Number of blows per surfacing, durations of surfacings, and durations of dives were all correlated. Whales spent about 21% of their time at the surface in July, and 23% of their time at the surface in September. There were fewer blows per surfacing, shorter surface times, and shorter dive times when whales were not feeding than when they were feeding. Intervals between successive blows were longer in non-feeding whales, but blow rate was not appreciably different with and without feeding.

Number of blows per surfacing and duration of surfacing increased with increasing water depth (from <20 to 80 m). However, dive duration did not change appreciably with depth in July. Blow rates by feeding whales increased in deeper water, indicating the need for whales to respire more as depth of dives increased. Time of day affected surfacing-dive-respiration characteristics differently in different months. Whales fed more from 18:00-21:00 than at other times of day in both months. There was a slight month to month variation in frequency of feeding: in July, about 79% of the time was spent feeding, whereas in September, only about 69% of the time involved apparent feeding. Calculations using estimates of feeding time and data on durations of surfacings and dives indicated that an average whale may have made about 198 feeding dives per 24-h period in July, and 164 feeding dives per 24-h period in September. During a surfacing, feeding whales moved about 50 m, and during a dive their net horizontal movement was about 90 to 100 m. Speed of movement averaged around 2 km/h, and was twice as fast 'at the surface (3.4 km/h) as underwater (1.7 km/h),

INTRODUCTION

The behavior of gray whales has been studied in Mexican calving lagoons (for example, Norris et al. 1977, in press; Swartz and Jones in press), and at points along the migration route near the North American coast (for example, Hatler and Darling 1974; Darling in press). Few long-term behavioral observations have been reported from the northern feeding areas, although Sauer (1963) described in detail the apparent courtship and copulations he witnessed off St. Lawrence Island, Bering Sea, Alaska.

As part of a study of the feeding ecology of gray whales, we spent parts of July and September 1982 observing behavior within 3 km of St. Lawrence Island (Fig. 1). Gray whales arrive at this island as early as May, and leave as late as November of most years (Pike 1962), although the main concentration of animals appears to be present from June through September (P. Gologergen, Savoonga, St. Lawrence Island, pers comm.). In order to help answer questions related to feeding ecology, we concentrated our effort on describing the surfacing, dive, and respiration patterns of whales. Surprisingly few data have been gathered on these aspects of behavior anywhere in the gray whales' range, although Sumich (1983) and Mate and Harvey (in press) gathered respiration information during northward migration; Murison et al. (in press) did similar work on gray whales summering off Vancouver Island, Canada. Nerini (1980) presents the only previous data on dive profiles of foraging gray whales off St. Lawrence Island.

The major intent of our behavioral investigations of gray whales was to determine amount of near-bottom feeding and associated respiration, surfacing and dive variables. We also investigated distance traveled at the surface and below the surface, and speed of travel. These data are being used by benthic ecologists to assess the importance of the northern Bering Sea as a primary summer feeding area of gray whales (Thomson and Martin, this report). Our data on durations of surfacings and dives are used to estimate the proportion of gray whales in the study area that were detected during aerial surveys conducted in July and September 1982 (Miller, this report).

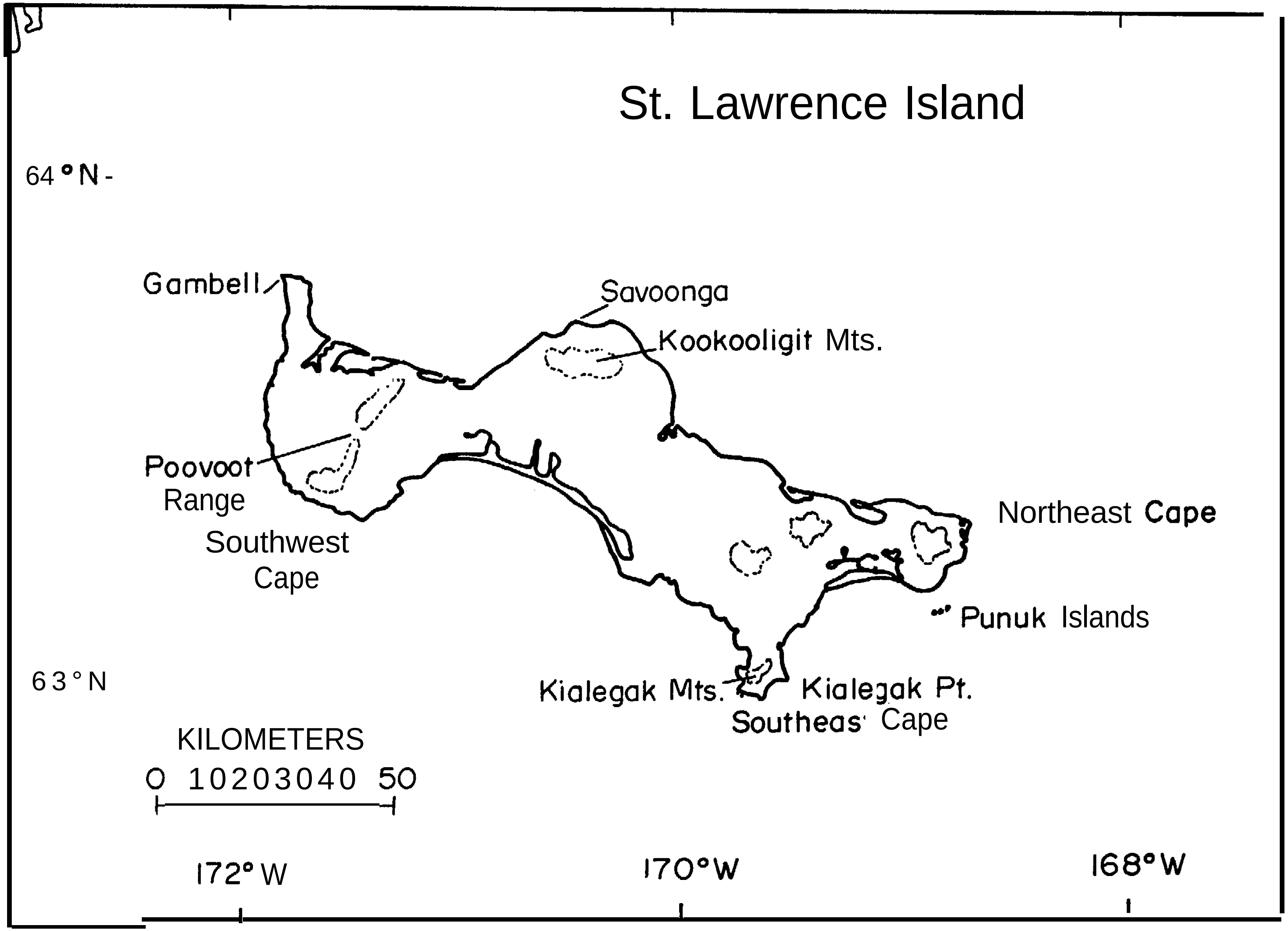

FIGURE 1. St. Lawrence Island, Bering Sea.

METHODS

In July and September 1982, the NOAA research vessels MILLER FREEMAN (length 65 m), and DISCOVERER (length 93 m), took us to the vicinity of St. Lawrence Island, Alaska, where most behavioral observations were carried out within 1 to 5 km of shore (Fig. 1). Although we watched whales from the flying bridge of MILLER FREEMAN (height above water 12 m), and the flying bridge and "aloft conning tower" of DISCOVERER (heights above water 15 m and 23 m, respectively), most observations were carried out from small vessels (4 to 8 m long) deployed from the research ships. We made detailed observations of behavior during 18 days: July 12-14, 16-21, and September 12, 16, 18-21, 23, 26, 27.

Behavioral observations were made from the large vessels while they were stationary and engaged in benthic ecology work (Thomson, this report), and from the small vessels while they were anchored, drifting, or slowly motoring within 300 m of whales. Three observers worked as a team (often with the casual help of a fourth observer); one to describe focal animals with the aid of binoculars; one to scan the surrounding area for number of whales, distances apart, direction of movement and general behavior; and one to record data and give feedback on what the other two observers might have forgotten to address. For focal animals, we systematically recorded durations of surfacings, all exhalations (termed blows), durations of dives, whether whales threw their tails out of the water upon diving, and our interpretation of general behavior.

Whales were often identified through distinctive pigment and other spot patterns and marks on their backs and/or tails. For such identified whales, we were able to determine dive durations. This technique of identification has been used successfully by Hatler and Darling (1974), Leatherwood (1974), and many other investigators.

We recorded a whale as feeding when it surfaced with mud coming off its body, or when birds landed at the surfacing site, and appeared to peck at substances in the water. The first characteristic was probably first described by Scammon (1869), and the latter in detail by Wilke and Fiscus

(1961) and Harrison (1979). In our experience, nearly all birds that landed at surfacing locations were black-legged **kittiwakes** **(Rissa tridactyla).** These were abundant off the cliffs on the west side of the island, but were seldom seen off Southeast Cape, where most of our observations were made. In the latter area, we had to rely mainly on presence of mud as evidence of feeding by the whales. Whales were scored as "possible feeding" if observed with mud at some point during the course of observation, but not upon each surfacing, as long as other aspects of their behavior pattern remained unchanged. Whales were assumed not feeding when we were close enough to be sure we could see mud if it were present and we did not see it, or when they were obviously socializing, traveling, or resting at the surface. Such negative data do not allow us to state for certain that feeding was not occurring, especially because feeding could have taken place in the water column without our knowledge.

Whales were considered socializing if they were within one-half body length of each other or were obviously interacting. We defined a group as whales within five body lengths of each other, but we realize that whales could be '*grouping"' by sound contact over longer distances. Resting whales were rarely seen, but when seen were quiescent at the surface for prolonged periods.

On 27 September, whales were observed from a 77-m high station near Kialegak Point, Southeast Cape (Fig. 1). Their positions and speeds of movement were plotted by the use of a Pentax TH 20D theodolite, or surveyor's transit, by a technique similar to descriptions of theodolite tracking by Würsig (1978) and Tyack (1981). These shore observations were coordinated by radio with those of observers in a small vessel.

All of the observations in this report are of "non-calf" whales. We did not obtain any data on whales that we could unequivocally call "young of the year". Our failure to recognize calves was probably because of (1) our usual low vantage point, (2) the frequent lack of any nearby whale for size reference, and (3) the fact that young are already quite large by late summer. We realize that we may have lumped data from young animals with our observations of non-calves.

Numerical data were analyzed with an Apple II+ home computer, a Hewlett-Packard 41 CV computer-calculator, and statistical techniques following mainly Sokal and Rohlf (1969) and Zar (1974).

RESULTS

General Description

Whales off St. Lawrence Island were generally alone, separated from their nearest neighbor by approximately 300 to 500 m. Most behavior appeared related to bottom feeding. We found in July that if we anchored near a feeding whale, it would stay near us, despite a current of 1 to 3 km/h. Thus, feeding whales apparently stay in roughly the same area for some time, possibly resisting current action. In July, we recognized two whales on subsequent days; one whale was sighted on 16 and 17 July and the other on 19 and 20 July. During each refighting, the whales were no more than 1000 m from the position where they fed on the previous day, and it is therefore likely that individual site tenacity during feeding is great. We have no such information for whales in September, when rough weather prevented us from anchoring or efficiently estimating distances covered by a particular whale. We also had no resightings of recognizable whales on different days in September.

In July, we obtained respiration and surfacing information on 158 whales, and only two were classified as socializing. In September, we obtained information on 53 whales, and nine of them were in social groupings. The difference between months in frequency of socializing was significant (chi^2 = 19.84 df = 1, $p<0.001$). Furthermore, whereas in July the two socializing whales were in groups of two, in September, five were in groups of two and four were in groups of three. In September, there were more incidence of socializing from 19-27 September (eight socializing whales among 25 whales) than during the early part of the month, 12-18 September (one socializing '*focal"' whale among 28 whales observed). Once again, the difference was significant (chi^2 = 7.57, df = 1, $p<0.025$), and the evidence appears strong that frequency of socializing increased toward the end of September, At the same time, feeding dives became shorter (to be detailed later), although feeding still took place. Ten of 158 focal whales observed in July were in groups of two (none in groups of three), while 15 of 53 whales in September were in groups of two (11 focal whales) or three (four focal whales). This difference was also significant ($chi^2 = 18.35$, $df = 1$, $p<0.001$). Overall, 14 of the 25 multi-whale groups were feeding, resting, or traveling rather than socializing.

Respiration and Surfacing Characteristics

The surfacing-dive cycle of the gray whale was quantified in terms of a period when the whale was below the surface, either swimming or feeding (duration of dive) and a period when the whale was at or near the surface (duration of surfacing). During each surfacing, we measured the frequency of exhalations (blows) and measured the interval between successive blows.

The blow interval, number of blows per surfacing, duration of surfacing, and duration of dive were measured 3503, 1050, 1062, and 905 times, respectively. Figure 2 presents the frequency distributions of these observations separated into the two months of field time. All variables approximated a normal distribution, and statistical comparisons with parametric tests were therefore possible.

The overall mean blow interval was 13.5 * s.d. 7.27 s (n = 3503), and was significantly shorter in July (mean = 12.6 ± 6.45, n = 1947) than in September (mean = 14.7 ± 8.02, n = 1556) ($t = 8.590$, $df = 3501$, $p<0.001$). Number of blows per surfacing and duration of surfacing were remarkably similar in July and September (Table 1), and the combined values for the two months were 4.2 ± s.d. 2.23 blows/surfacing (n = 1050), and 0.89 ● s.d. 0.728 min surface time (n = 1062). The two values were also closely correlated, with greater numbers of blows per surfacing during longer surfacing; ($r = 0.636$, $df = 594$, $t = 20.08$, $p<0.001$ in July; $r = 0.851$, $df = 450$, $t = 34.44$, $p<0.001$ in September). Durations of dives tended to be longer in July than in September ($t = 4.406$, $df = 903$, $p<0.001$). Dive duration was correlated with surfacing duration, both in July ($r = 0.236$, $df = 441$, $t = 5.10$, $p<0.001$), and in September ($r = 0.374$, $df = 375$, $t = 7.83$, $p<0.001$).

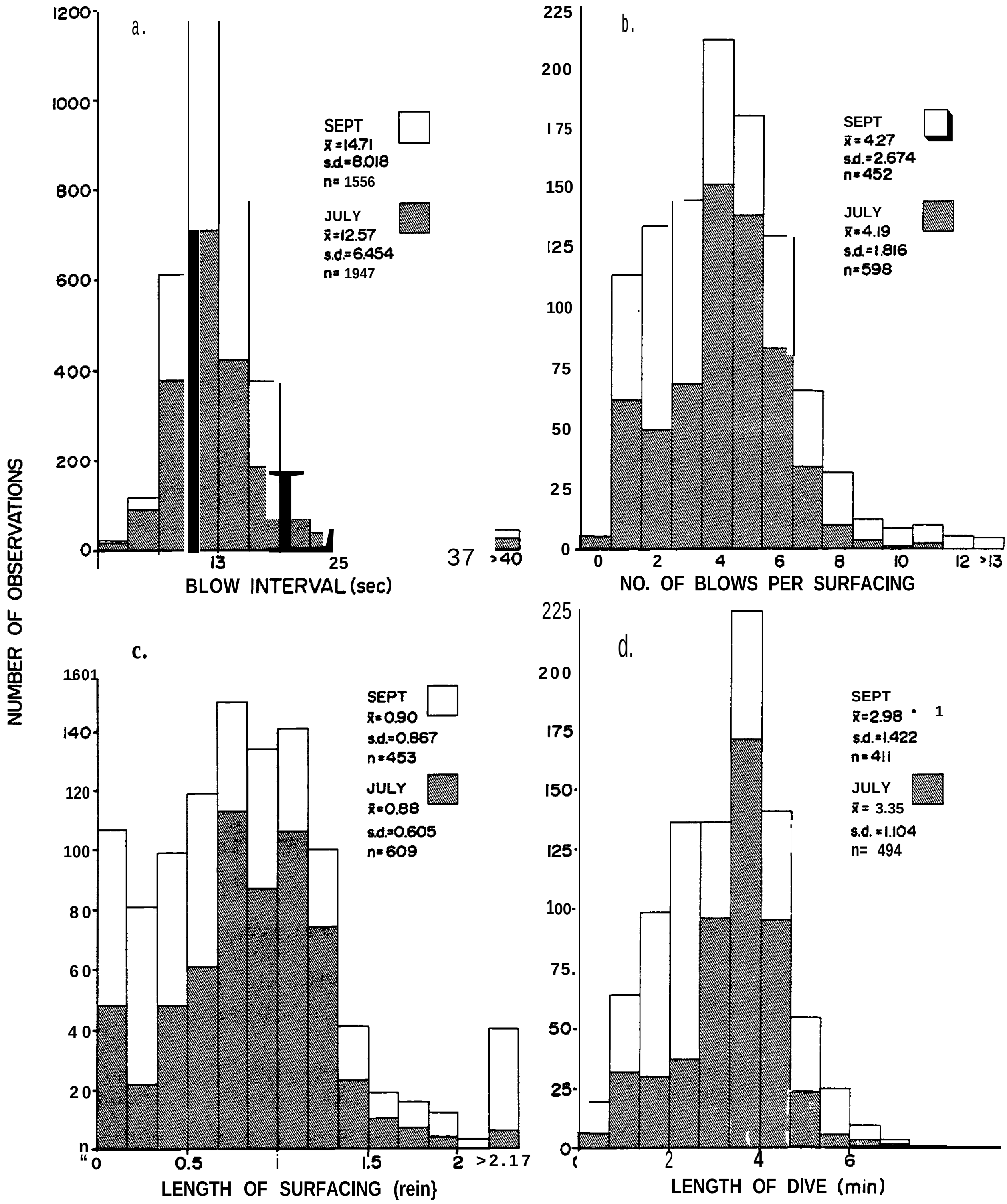

FIGURE 2. Frequency distributions of the four respiration, surfacing and dive variables.

Table 1. Summary statistics for the principal respiration, surfacing and dive variables.

	Blow interval (s)			Number of blows per surfacing			Duration of surfacing (rein)			Duration of Dive (rein)		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Overall :												
July	12.6	6.45	1947	4.2	1.82	598	0.88	0.604	609	3.35	1.104	494
September	14.7	8.02	1556	4.3	2.67	452	0.90	0.867	453	2.98	1.422	411
July-September	13.5	7.27	3503	4.2	2.23	1050	0.89	0.728	1062	3.18	1.271	905
July :												
Feeding	12.2	5.53	483	4.4	1.50	141	0.93	0.393	141	3.68	1.043	116
Possible feeding	12.6	4.74	859	4.5	1.75	247	0.91	0.429	260	3.42	0.976	239
Not feeding	15.2	12.58	110	3.0	2.37	51	0.49	0.561	56	2.43	1.236	46
September:												
Feeding	16.8	9.72	248	6.2	3.18	45	1.38	1.039	45	3.50	1.428	41
Possible feeding	13.8	6.78	877	4.0	2.48	276	0.80	0.737	277	3.01	1.337	264
Not feeding	18.0	9.85	152	3.3	2.76	64	0.83	1.220	64	1.91	1.1,20	64
July - Depth:												
1-20 m	13.3	9.72	243	3.1	1.52	116	0.72	0.853	118	3.22	1.102	95
21-40 m	12.6	5.16	1298	4.3	1.79	384	0.91	0.533	391	3.34	1.156	314
41-60 m	21.2	18.98	39	5.1	3.23	8	1.12	0.826	9	1.48	0.671	5
61-80 m	12.2	5.12	133	5.2	2.22	29	1.09	0.670	30	3.28	1.247	19

Continued. . .

Table 1. Concluded.

	Blow interval (s)			Number of blows per surfacing			Duration of surfacing '(rein)			Duration of Dive (rein)		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
September - Depth:												
1-20 m	15.0	9.47	560	3.3	1.96	239	0.63	0.695	239	2.38	0.996	218
21-40 m	16.7	6.36	464	6.4	3.13	78	1.63	1.018	79	4.40	1.413	74
41-60 m			0	-	-	0	-	-	0	-	-	0
61-80 m			0	-	-	0	-	-	0	-	-	0
July - Time of Day:												
5-9	13.1	7.95	408	4.4	1.77	116	0.97	0.465	116	3.32	1.084	77
10-13	13.2	6.70	776	4.5	1.84	214	1.04	0.803	220	3.46	1.049	182
14-17	11.7	4.38	359	4.2	1.46	108	0.84	0.317	112	3.58	0.834	89
18-21	11.7	5.63	398	3.5	1.90	160	0.63	0.424	167	3.10	1.273	146
September - Time of Day:												
5-9	12.1	3.19	18	3.8	0.84	5	0.81	0.386	5	3.44	0.985	7
10-13	15.9	10.25	287	3.0	2.25	132	0.65	0.935	132	2.18	1,060	130
14-17	14.7	8.28	826	4.3	2.48	239	0.89	0.767	239	3.06	0.226	203
18-21	14.1	5.38	424	6.3	2.74	76	1.36	0.889	77	4.19	1.256	71

It is especially useful, when undertaking aerial surveys to determine numbers of whales, to know what proportion of time a whale spends at the surface, and is therefore visible. In July, average surface time divided by average duration of a surfacing-dive cycle (0.88/[0.88 + 3.35] rein) yielded a surface time proportion of 0.208. In September, when dives were somewhat shorter, the average time at the surface (0.90/[0.90 + 2.98] rein) yielded a surface time proportion of 0.232. These values give an indication of the probability of detecting a gray whale at a point in time along an aerial survey transect line, but the horizontal distance of the whale from the aircraft and the speed of the aircraft must also be taken into account (Miller, this report).

We calculated the number of blows per unit time, or blow rate, by analyzing the number of blows for surfacing-dive cycles when all blows were seen and total length of the surfacing and dive was known. In July, there were 1833 blows in the 1839.1 min total duration of 434 surfacing-dive cycles, for a blow rate of 0.997 blows/rein. In September, there were 1612 blows in 1436.7 min of 377 surfacing-dive cycles, for a blow rate of 1.122 blows/rein.

Relationships to Feeding

We divided our observations into (1) known feeding, (2) possible feeding, (3) not feeding, and (4) other behavior. Surfacing-dive characteristics of the first three categories of whales were summarized.

Blow intervals tended to be longer when whales were not feeding than when they were feeding or possibly feeding. This was so both in July (F = 11.99, df = 2, 1449, $p<0.001$) and in September (F = 27.51, df = 2, 1274, $p<0.001$) (Fig. 3a). Number of blows per surfacing also differed among the three feeding categories for July (F = 16.80, df = 2, 382, $p<0.001$), with fewer blows per surfacing while whales were not feeding, and more during possible and definite feeding (Fig. 3b). Duration of surfacings showed the same trend, which is not surprising because of the close relationship between duration of a surfacing and the number of blows during that surfacing (feeding characteristic comparisons: July F = 23.58, df = 2, 454, $p<0.001$;

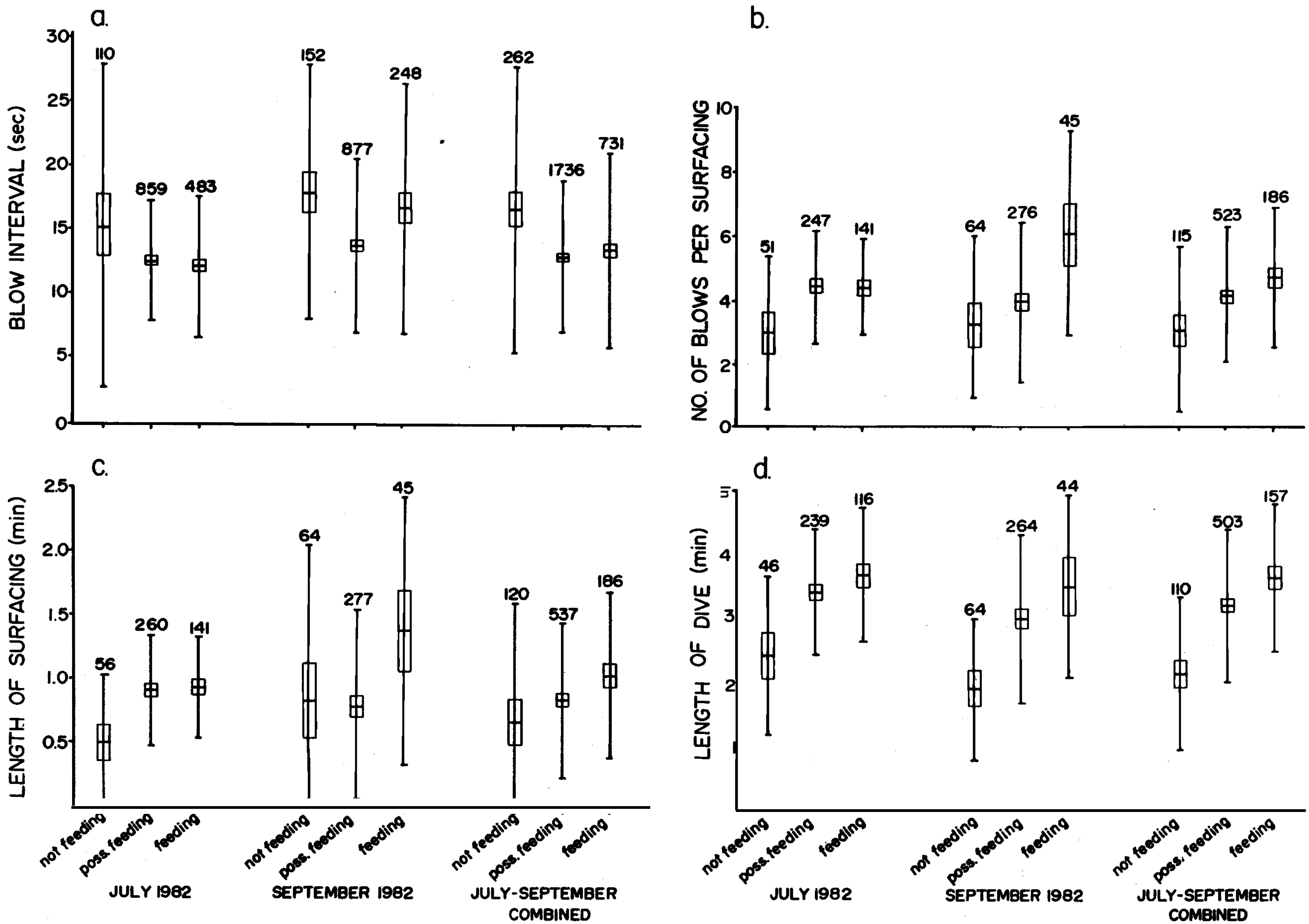

FIGURE 3. Respiration, surfacing and dive variables by feeding category Bars represent 1 s.d. on each side of the mean, and boxes represent 95% confidence intervals.

September F = 8.85, df = 2, 383, $p<0.001$). Duration of dives was also lowest for non-feeding whales, and highest for feeding whales (Fig. 3d; July F = 24.84, df = 2, 398, $p<0.001$; September F = 23.29, df = 2, 366, $p<0.001$). Of the four variables, dive time was the one that differed most consistently between whales that were and were not feeding. Duration of dives may thus be a useful indicator of feeding. This concept will be explored further in the "Amount of Feeding"' section.

Blow rates did not vary greatly with feeding category; in July, the blow rate for feeding whales was 0.974 blows/rein (114 surfacing-dive cycles), and that for non-feeding whales was 0.976 blows/rein (41 surfacing-dive cycles). In September, the feeding blow rate was 1.288 blows/rein (41 surfacing-dive cycles), and the non-feeding blow rate was 1.186 blows/rein (58 surfacing-dive cycles).

Relationships to Depth of Water

Whales were found around St. Lawrence Island in water depths ranging from 6 to 79 m. We divided this range into four depth categories as shown in Figure 4. Blow intervals were correlated with depth (Fig. 4a). Number of blows per surfacing and the correlated duration of surfacing increased with increasing depth, and the change was significant for both characteristics during both months (Number of blows: July F = 17.56, df = 3, 533, $p<0.001$; September t = 10.37, df = 315, $p<0.001$. Duration of surfacings: July F = 4.28, df = 3, 544, $p<0.001$; September t = 9.78, df = 316, $p<0.001$).

Duration of dives, on the other hand, did not show a consistent increase with increasing depth in July. The analysis of variance statistic is marginally significant only because of five short dives from one animal in 41-60 m water depth (Fig. 4d) (F = 4.475, df = 3, 429, $p<0.05$). According to the SNK multiple-comparison test, the value for 41-60 m is significantly lower than values from all other-depth categories at $p<0.01$; values for all other pairs of depths were not significantly different. In September, durations of dives were determined only for the two shallower depth categories. Dives in 21-40 m depth were significantly longer than those in 1-20 m (t = 13.44, df = 290, $p<0.001$).

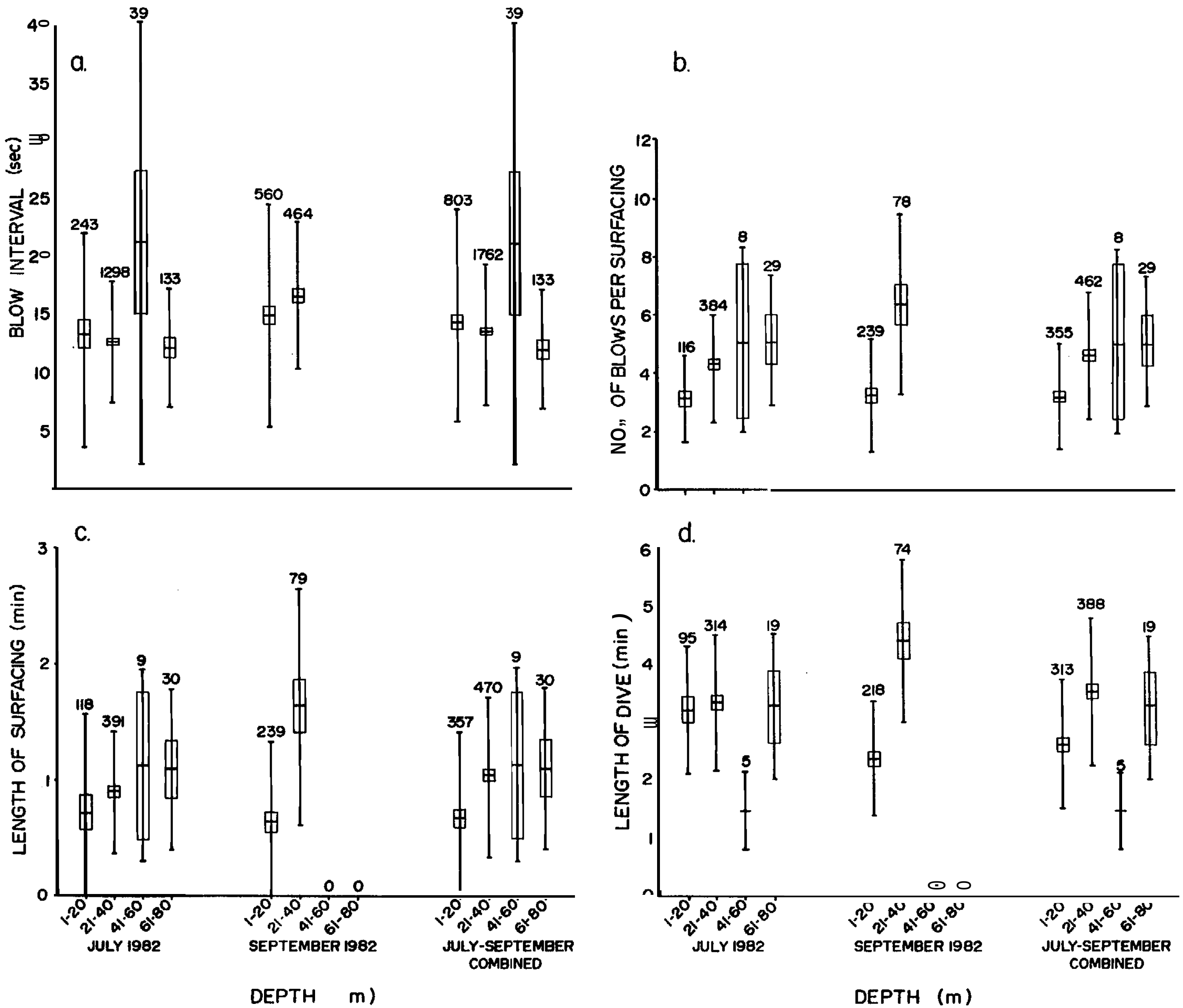

FIGURE 4. Respiration, surfacing and dive variables by depth of water. Statistics displayed as in Fig. 3.

To test whether the apparent relationship between durations of dives and depth may have been confounded by differences in feeding during the two months, we examined durations of definite feeding dives at various depths. In July, there was no longer a significant difference in durations of dives in waters of different depths, mainly because there were no feeding dives in the 41-60 m category ($F = 0.176$, $df = 2, 107$, ns). However, in September the difference in durations of feeding dives in waters 1-20 m and 21-40 m depth was again significant ($t = 5.15$, $df = 36$, $p<0.001$). Therefore, the month to month difference in depth effect does not appear to be due solely to differential amounts of feeding. In any case, the relationship between duration of dive and depth is not as linear or consistent as that between duration of surfacing and depth (compare Fig. 4c to Fig. 4d).

In July, with increasing depth there was a tendency for increased surface time and increased number of blows per surfacing, but little change in dive time. Thus, it is not surprising that the blow rate was higher in deeper water during that month. The July blow rates of feeding and possibly feeding whales were 0.794 blows/rein (53 surfacing-dive cycles) in 1-20 m water depth, 1.043 blows/rein (212 surfacing-dive cycles) in 21-40 m depth, and 1.190 blows/rein (11 surfacing-dive cycles) in 61-80 m depth. In September, the increase was only slight: 1.085 blows/min (178 surfacing-dive cycles) in 1-20 m depth, and 1.116 blows/rein (56 surfacing-dive cycles) in 21-40 m depth.

Our results of differential amounts of respiration in different water depths are particularly interesting, for we are reasonably certain that whales dove to the depths indicated while feeding. Therefore, the differential blow rates are apparently related to depth of dive.

Relationships to Time of Day

The four basic respiration and surfacing characteristics all differed significantly among the four i-h categories that we compared (analysis of variance $F>7.0$, error df from 448 to 1937, $p<0.001$), but the trends were different for the two months, and for combined data, almost cancel each other (Fig. 5). In July, number of blows per surfacing, duration of surfacings,

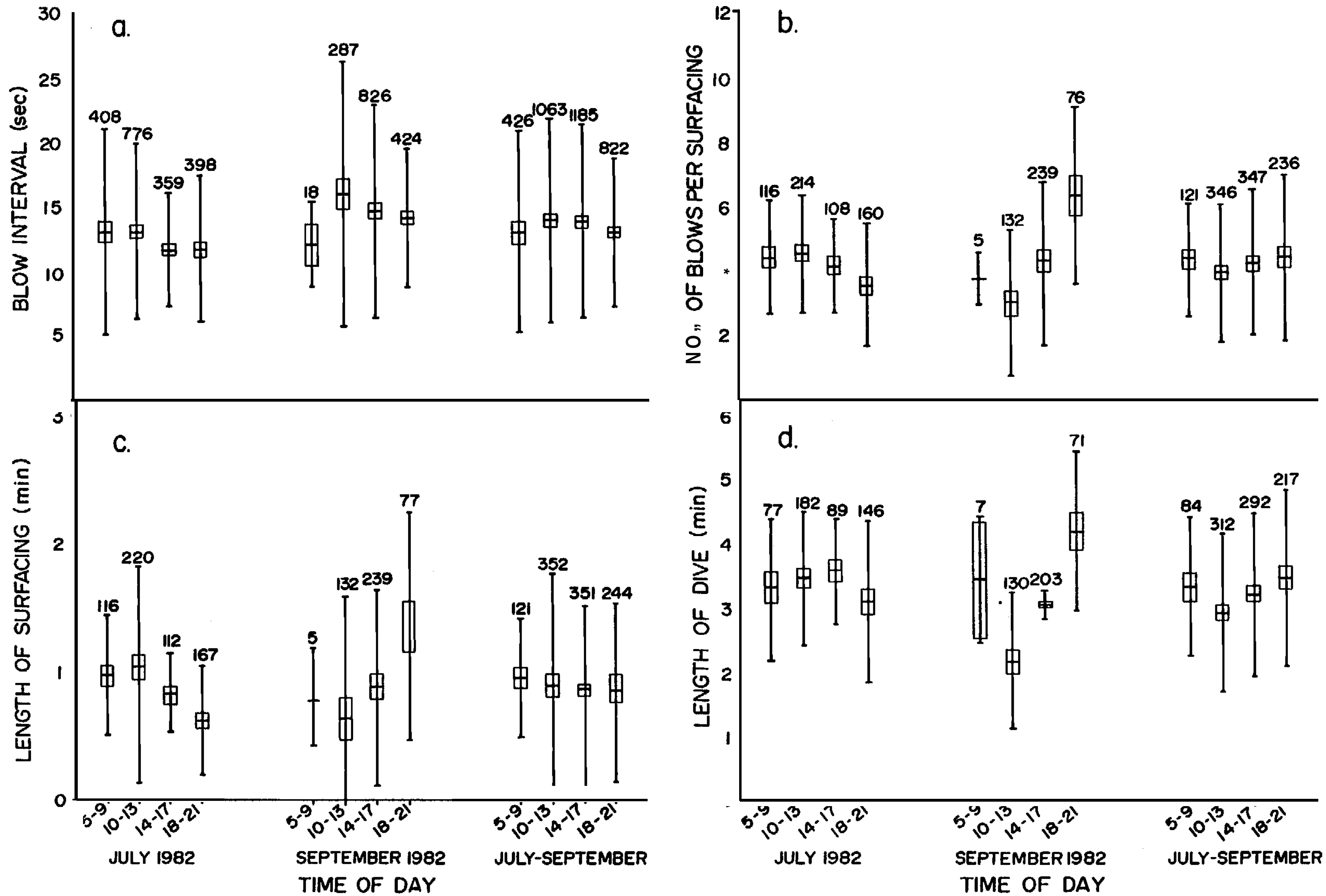

FIGURE 5. Respira=ion, surfacing and dive variables by time of day, divided into four 4-h categories. Time is Anchorage time, GMT-9 h. Statistics displayed as in Fig. 3.

and duration of dives were greater during midday, but in September, this trend was reversed. Other variables such as feeding behavior and depth of water probably were more important determinants of these characteristics.

To determine whether there was a relationship between amount of feeding and hour of day, we compared number of known feeding dives to total number of dives (Table 2). In both months, known feeding dives comprised a larger fraction of all dives during the evening (18:00-21:00) than earlier in the day. The ratios in Table 2 are intended only for comparative purposes between hours and months, because they grossly under-represent the actual frequency of feeding. The "No. of Dives" column only considers those whales that surfaced with mud, plus surfacings when kittiwakes landed behind the whale. The "possible feeding'* category is not included.

Relationships to Time of Season

There was no consistent trend in amount of feeding across dates within either month, but there was much more known feeding in July than in September (Table 3). The duration of feeding dives was relatively stable from day to day in July, but in September, feeding dives became shorter at the end of the season (Fig. 6). Table 3 and Figure 6 do not represent all possible feeding dives because they consider known feeding only, as explained under "Time of Day". As mentioned previously, the frequency of socializing increased toward the end of September.

Amount of Feeding

With the available information on surfacing and dive characteristics, we can make reasonably good estimates of the proportion of time whales spend feeding. We make the assumption that we are just as likely to gather data on whales feeding as opposed to some other activity, and that our determination of feeding, possible feeding, and not feeding reflected actual behavior accurately.

Table 2. Relative frequency of feeding dives at different times of day in July and September.

Time	No. of Feeding Dives (1)	Total No. of Dives (2)	Ratio (1)/(2)
July:			
5-9	11	77	0.143
10-13	44	182	0.242
14-17	13	89	0.146
18-21	47	146	0.322
September:			
5-9	0	7	0
10-13	5	130	0.038
14-17	18	203	0.089
18-21	18	71	0.254
July and September:			
5-9	11	84	0.131
10-13	49	312	0.157
14-17	31	292	0.106
18-21	65	217	0.300

Table 3. Relative frequency of feeding dives on different dates.

Day	No. of Feeding Dives (1)	Total No. of Dives (2)	Ratio (1)/(2)
July:			
12	26	73	0.356
13	6	19	0.316
14	0	5	0
16	6	80	0.075
17	39	95	0.411
18	9	29	0.310
19	18	78	0.231
20	2	44	0.045
21	9	71	0.127
Total	115	494	0.233
September:			
12	1	26	0.038
16	1	7	0.143
18	14	46	0.304
19	0	62	0
20	0	4	0
21	11	73	0.151
23	4	13	0.308
26	2	28	0.071
27	8	152	0.053
Total	41	411	0.098

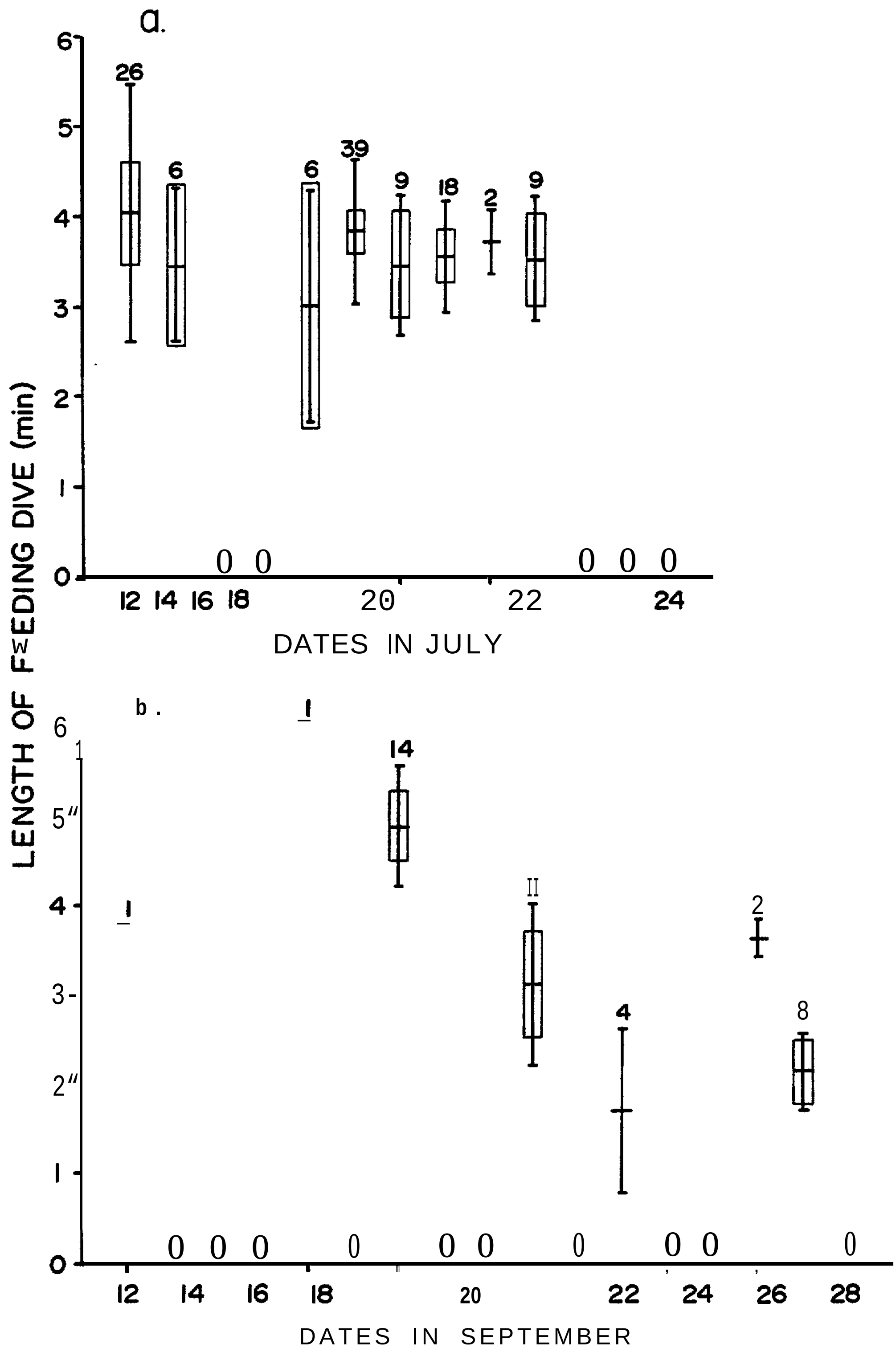

FIGURE 6. Duration of feeding dives during days with observations in July and September 1982. Statistics displayed as in Fig. 3.

In July, we watched whales for a total of 2190.82 rein, and we watched whales definitely feeding for 558.01 min. This gives a feeding proportion of 0.255 total time, considering only definite feeding dives and associated surfacings. Many of the possible feeding observations also represent feeding. If we add this time (1053.98 rein) to the definite feeding time, we have a total of 1611.99 min total possible feeding time. The possible feeding proportion is then 0.736 total time, and our range is from a low of 0.255 to a high of 0.736 total time spent feeding.

Similar calculations for September result in a range of 0.126 total time, considering only definite feeding, to 0.748 total time, considering both definite and possible feeding.

Although it is difficult to say how much feeding occurred within the "possible feeding" category, it was our subjective impression that in July, about three-quarters of the possible feeding time represented feeding, while in September, somewhat less than three-quarters represented feeding. The durations of dives appear to be a very good indicator of presence or absence of feeding. In July, the mean feeding dive was 3.68 min in duration, and in September, it was 3.50 rein, with small standard deviations in both cases (± 1.043 and ± 1.428 rein, n = 116 and 41, respectively). Non-feeding dives in JUly were 1.25 min shorter than feeding dives, and non-feeding dives in September were 1.59 min shorter than feeding dives. The mean durations of possible feeding dives were intermediate. We speculate that a ratio composed of the difference between the mean duration of non-feeding dives and of possible feeding dives divided by the difference between the mean duration of non-feeding dives and definite feeding dives represents the proportion of possible feeding dives than should actually be classified as feeding (here called "probable feeding"). For July, this value is 0.79 (proportion of possible feeding dives that are probable feeding dives), and for September, it is 0.69. These values are remarkably close to our subjective impression of the situation.

These calculated proportions may be used to adjust the possible feeding time to probable feeding time, and to add this new value to definite feeding time. The total probable feeding time for July is then 1390.65 rein, and the proportion of time spent feeding is estimated to be 0.635 total time (total probable feeding time over overall time). For September, this value is 0.555 total time.

We observed feeding throughout the day from 05:00 to 21:00 h, but we have no detailed" information on possible feeding or on surfacing-dive patterns during the night. If we assume that feeding dives continue at night, and that the average length of the surfacing-dive cycle is approximately the same as during the day, then approximately 312 feeding dives are possible in 24 h in July (4.61 min per feeding dive cycle, 1440 min per 24 h). Because the proportion of time spent feeding is approximately 0.635 total time, we may expect that one whale averaged about 198 (312 x 0.635) feeding dives per 24 h in July. In September, approximately 295 feeding dives were possible in 24 h, and the average number of feeding dives by one whale in 24 h was 164 (295 x 0.555). This is somewhat less than the amount of feeding seen in July, and agrees well with our impressions (before analysis of the data) concerning the relative amount of feeding in September vs. July. For a summary of the calculations, see Appendix I.

Our calculations are only as good as our assumptions. We are reasonably certain that we were not biased toward or away from gathering information on feeding whales. We also believe that duration of dive can be used as an indication of bottom feeding, and thus our correction factor to convert "possible dives" to "probable dives" is valid as a first approximation. We are less certain of the amount of feeding and the dive durations during the night, however, and therefore suggest that the final estimates of "number of feeding dives per 24 h" be treated with caution.

Distance Traveled and Speed of Travel

As an aid to describing the behavior of whales, we estimated distance traveled while whales were at the surface, and the net horizontal distance traveled during dives. These estimates were obtained on occasions when whales were within about 150 m of the boat and the boat was stationary.

In July, overall distance traveled during surfacing was 57 ± s.d. 55.0 m (n = 32), and minimum horizontal distance traveled during dives was 95 ● 82.9 m (n = 93). The difference between distance covered above and below the surface was significant ($t = 2.42$, $df = 123$, $p<0.02$). In September, surface distance was considerably shorter, at 30 * 23.8 m (n = 25)* Dive distance was comparable to the July value, 92 ± 88.1 m (n = 30), and the difference between surface and dive distance was again significant ($t = 3.40$, $df = 53$, $p<0.002$).

On 27 September, we obtained exact theodolite measurements of distances traveled at the surface five times, and minimum distance traveled below the surface eight times, all on one feeding whale in 6 m water depth. Distance at the surface was 36 * 31.6 m (n = 5), and distance below the surface was 54 ± 22.3 m (n = 8). Estimates made at the time this whale was being observed agree with the calculated distances. It is therefore likely that this whale traveled especially small distances while diving. This may have been due to the exceptionally shallow water in which the whale was diving, although we have no proof for this assertion.

Table 4 summarizes distance traveled according to category of feeding. There are too few values for meaningful comparisons of distance traveled during feeding and during non-feeding dives. However, feeding whales surfaced an average of about 90 to 100 m from where they submerged. We do not know whether the whales' tracks underwater were in a straight line.

On 27 September, theodolite-generated tracks were obtained for three feeding whales (including the above-described whale). These three whales remained in an area 3700 m north-south, and 700 m east-west for the four hours of observation. This restricted movement was accomplished by whales moving northerly for about 60 rein, then moving in a southerly direction for about 60 rein, and then reversing direction again. This movement kept the whales close to 6 m depth at all times because the depth contour line ran north-south. The regular nature of feeding behavior is reflected in the similarity of the average speed of movement for each of the three whales: Whale A 2.3 ●s.d. 2.18 km/h, n = 77; Whale B 2.3 * 1.75 km/h, n = 42; Whale C 2.8 ± 2.23 km/h, n = 34. For whale A, speeds were obtained separately for some surface and below-surface movements: 3.4 ± 2.14 km/h (n = 5) at the SUrfaCe and 1.7 ± 0.66 km/h (n = 8) below the surface. It thus appears that net horizontal speed while diving was slower, but the result is a minimum

Table 4. Estimated distances traveled during surfacings and minimum distances traveled during dives, subdivided by feeding category and month.

	July			September		
	mean	s.d.	n	mean	s.d.	n
Surfacing Distance (m)						
Not feeding	150		1	17	28.9	3
Possible feeding	47	36.4	24	31	21.0	18
Feeding	69	79.8	9	33	41.6	3
Dive Distance (m)						
Not feeding			0	138	94.7	4
Possible feeding “	83	45.0	62	68	55.9	21
Feeding	100	45.6	24	93	100.7	3

speed, because it assumes a straight line between the points of diving and surfacing, and ignores the vertical movement of the whale. The result appears reasonable, however, for we might expect whales to move forward slowly while feeding on benthic or epibenthic invertebrates.

DISCUSSION

Our observation that individual whales spent hours and, on at least two occasions, over a day feeding in a small area indicates some site tenacity. We do not know whether individual feeding ranges are actually well defined for most animals. The fact that feeding whales were generally far apart from each other hints at (but in no way proves) the possibility of feeding territories. Similar site tenacity has been observed for feeding gray whales off Vancouver Island, B.C., by Darling (in press) and Murison et al. (in press).

We encountered mainly what we judged to be "adult" whales, although some possible juveniles were perhaps four-fifths the size of most others. Zenkovitch (1937), Votrogov and Bogoslovskaya (1980), and Bogoslovskaya et al. (1981) provide data which show that young animals often forage in different areas than older *ones,* and this kind of size separation may be responsible for our apparent lack of sightings of young gray whales. It is also possible, as mentioned earlier, that we saw but failed to recognize some young.

Little socializing occurred in July, but more socializing was seen during the latter half of September. The two socializing incidence in July involved rolling at the surface and nudges and pushes. They appeared similar to (although not as boisterous as) the descriptions of apparent precopulatory activity witnessed along the west shore of St. Lawrence Island by Sauer (1963) and Fay (1963). Whales were more often in groups of two to three in September than in July. Zimushko and Ivashin (1980) also found that gray whales feeding along the Russian coast were generally alone, although groups of two to three occurred as well. They did not discriminate by time of season. We had the impression that behavior changed more often from feeding to socializing or traveling in September than in July. This heightened amount of change in general behavior may be part of a **migratory unrest" preceding the migration southwards.

Surface time, number of blows per surfacing, and dive time were all correlated. "Similar results were obtained on bowhead whales, the only other baleen whale species for which detailed respiration and surfacing characteristics have been reported (Würsig et al. 1982, 1983). Surface time of gray whales in July was 21% of total time, and in September was 23% of total time. This is remarkably similar to the 24% surface time reported for mainly feeding bowhead whales in the Beaufort Sea in August (Würsig et al. 1983). These results are very different from the proportional surface times of gray whales near their wintering areas off Baja California and during migration; Harvey and Mate (in press) found that whales radio-tagged in Laguna San Ignacio, Mexico, were at the surface only 4.5% of the time. Detectability of gray whales during aerial surveys would clearly be very different in these two situations.

While feeding, gray whales had longer dives, longer surface times, and more blows per surfacing than while not feeding. However, the blow rate, or number of respirations per unit time, did not change appreciably. Number of blows per surfacing and duration of surfacings also increased in deeper water but--at least in July--duration of dives did not increase. Blow rates were higher in deeper water, which suggests that whales are more stressed physiologically during deep dives, even at depths only 20 m deeper than their shallowest dives (around 6 m depth, or one-half body length of a whale). This is a new and potentially important concept warranting further study. Sumich (1983) found a blow rate of 0.72 blows per minute in whales migrating south past California, and a blow rate of 0.5 blows per minute in essentially stationary whales in Laguna San Ignacio. These rates are appreciably lower than the blow rates of whales feeding in water >20 m deep (around 1 blow/rein), but comparable to the blow rate of whales feeding in water <20 m during July (0.794 blows/rein). Harvey and Mate (in press) calculated a blow rate of approximately 0.58 blows/rein in stationary whales and 1.00 blows/rein in a whale swimming at 4 km/h. The latter value is higher than the result for migrating whales observed by Sumich (1983). The difference may, in part, be due to methodology. Harvey and Mate used a radio transmitter and Sumich used visual observations. The blow rate of non-calf bowhead whales in the Beaufort Sea was approximately 0.70 blows/rein (Würsig et al. 1983).

It is difficult to compare the individual surfacing, respiration, and dive variables of whales on the feeding grounds in summer with those in other areas at other times. Feeding whales generally dive for some time, and then surface for some time while blowing repeatedly. During migration and in winter, however, they only surface to breathe. This is well exemplified by data from Harvey and Mate (in press): surface time of whales in Laguna San Ignacio was only 0.07 + 0.1 min (no sample size given), as opposed to 0.89 ± s.d. 0.728 min (n = 1062) during our study. However, only one blow occurred during each brief surfacing in the wintering area, whereas we observed an average of about 4 blows per surfacing.

Nerini (1980) published raw data concerning 20 dives of gray whales foraging near St. Lawrence Island. Our analysis of these data gives a mean dive time of 3.53 min (s.d. = 1.053 rein, n = 20), close to our July and September combined mean of 3.63 ± 1.153 min (n = 157) for dives by feeding whale. Nerini also presented data on blow intervals and surface times, but the numbers were apparently not gathered systematically, and comparisons are not possible. Dive data in Nerini (1980) were gathered in 1977 and 1980, but there' is no indication of time, depth of water, or other variables.

We calculated the frequency of feeding, as evidenced by gray whales surfacing with mud or by the presence of birds. Our corrected values (including estimates of feeding when mud could not be seen) indicate that whales fed about 79% and 69% of the time in July and September, respectively. This is less than the "total feeding" assumed by earlier researchers, but is reasonable in light of recent investigations on bowhead whales in which socializing and travel, apparently without feeding, occur on the feeding grounds in the Beaufort Sea (Würsig et al. 1982). Whales are social mammals with large behavioral repertoires, and they do not totally extinguish all other behaviors in favor of a single behavior.

During the present investigation, speed of travel of feeding whales was determined accurately on only one day. It was around 2 km/h for the three whales measured, and surface speeds were twice as high as apparent dive speeds. Mate and Harvey (in press) estimated speeds of 3 to 4 km/h for northward migrating gray whales, whereas Leatherwood (1974) obtained values of 2.6 to 2.9 km/h. The southward migration is generally thought to be faster; Sumich (1983) measured one whale's speed as 15.5 km/h, but this was probably-during particularly rapid movement. Thus , the movements of whales in the feeding area around St. Lawrence Island generally appear to be more leisurely than those of migrating whales, and it is interesting that their blow rates are nevertheless higher; this is presumably related to diving deeper, as conjectured previously.

Whales moved a net distance of about 100 m below the surface while feeding, and moved about one-half that distance at the surface. Such data are fraught with uncertainty, however, for we do not know what the specific current regime was below the surface during these measurements, or whether whales below the surface traveled in a straight line. Thomson and Martin (this report) discuss the physical record of feeding in the St. Lawrence Island area, which consists of furrows and other indentations, and estimate how much biomass may be taken in by a foraging whale per dive.

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APPENDIX I. CALCULATIONS INVOLVED IN ESTIMATING THE NUMBER OF FEEDING DIVES OF AN AVERAGE GRAY WHALE AROUND ST. LAWRENCE ISLAND, ALASKA, IN JULY AND SEPTEMBER 1982.

July

Mean duration of feeding dive = 3.68 min

Mean duration of feeding surfacing = 0.93 min

4.61 min per feeding dive cycle.

There are 1440 rein/24 h.

1440/4. 61 = 312 feeding dives possible/24 h.

Mean duration of feeding dive = 3.68 min

1.25 min difference

Mean duration of non-feeding dive = 2.43 min

0.99 min difference

Mean duration of possible feeding dive = 3.42 min

.99/1 .25 = O. 79; therefore, we speculate that 79% of possible feeding dives are actual feeding dives, and we call these "probable feeding dives*'.

Overall time observed = 2190.82 min

Feeding time observed = 558.01 min

Possible feeding time observed = 1053.98 min

x **0.79**

= 832.64 probable feeding time

+ 558.01 definite feeding time

Total probable feeding time = 1390.65 min

1390.65/2190.82 = 0.635 proportion of time spent feeding.

Because 312 feeding dives are possible/24 h, 312 x 0.635 = 198 feeding dives for a whale/24 h.

(Or, 1440 rein/24 h x .635 = 914.4 feeding rein, ÷ 4.61 min per feeding cycle = 198 feeding dives/24 h.)

APPENDIX I. (continued)

September

Mean duration of feeding dive = 3.50 min

Mean duration of feeding surfacing = 1.38 min

4.88 min per feeding dive cycle.

There are 1440 rein/24 h.

1440/4.88 = 295 feeding dives possible/24 h.

Mean duration of feeding dive = 3.50 min

1.59 min difference

Mean duration of non-feeding dive = 1.91 min

1.10 min difference

Mean duration of possible feeding dive = 3.01 min

1.10/1.59 = 0.69; therefore, we speculate that 69% of possible feeding dives are actual feeding dives, and we call these "probable feeding dives".

Overall time observed = 1631.53 min

Feeding time observed = 205.60 min

Possible feeding time observed = 1015.41 min

x 0.69

= 700.63 probable feeding time

+ 205.60 definite feeding time

Total probable feeding time = 906.23 min

906/1631.53 = 0.555 proportion of time spent feeding.

Because 295 feeding dives are possible/24 h, 295 x 0.555 = 164 feeding dives for a whale/24 h.